The Pores of the Libriform Tissue.*

By Emily L. Gregory, Ph. D.

The results of the investigations in this direction served, in most instances, to confirm this supposition. Some care was taken to discriminate between small tracheæ and tracheids by use of macerated preparations. These attempts were not wholly satisfactory, owing to the impossibility of examining every separate cell. They served, however, to prove that in some instances the cells referred to by anatomists as tracheids, are really small tracheæ. For example, in *Robinia*, a large number of tracheid-like cells were found to communicate directly with each other by means of a circular opening in the partition wall. These two classes, small tracheæ and tracheids, seem to pass into each other here, by gradual transition stages, some being found to possess an opening at one end, thus communicating directly with the next cell, while at the other end no trace of an opening could be found.

Enough examples were studied to show that great variety exists in the number of elements of different woods. In *Quercus*, as before described, all the elements occur, so also in *Ligustrum*. Others were found to lack one or more, as *Ribes*, which lacks the thin-walled tracheids; *Comarum*, the simple-pored libriform; *Berberis*, the bordered-pored libriform, and also the wood parenchyma. Quite a large number have only large and small tracheæ; such are *Populus*, *Salix*, *Acer*, *Fraxinus* and others. Here occurs the difficulty before mentioned, of deciding accurately between tracheids and small tracheæ. In many woods where openings were found between the cells it was only by the most careful manipulation, and it is impossible to say with certainty that they fail entirely in any of the above mentioned cases. On the other hand, when they are found to exist in any part of the specimen under consideration, we can only infer that they exist throughout in the same element.

Only two examples were found which contained only large tracheæ and simple-pored libriform. These are *Betula alba* and *Corylus Avellana*. Here the tracheæ appear to be of a nearly

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uniform size, no small ones being present. In these two instances it must be inferred that either the simple-pored libriform cells do contribute in no small degree to the passage of water, or that the local needs are satisfied by some arrangement of the numerous large tracheæ. Although we have, at the beginning, excluded the consideration of the cells of the medullary rays and wood parenchyma, as not materially affecting the question of the nature of the libriform tissue, the suggestion may be allowed here, that a factor of such importance in the water transport, as this probably is, may come in play in a somewhat different manner here than in cases where the number of elements is greater.

The simplest woody tissue was found in *Veronica Andersoni;* a woody stem of two years' growth was found to contain only large and small tracheæ and simple-pored libriform, and no medullary rays nor wood parenchyma. In one year growths of *Chelone* and *Digitalis* the same structure was found, but the woody growth was not so well developed. The small tracheæ here might easily be mistaken for tracheids, and it is not possible to say with absolute certainty that all of these are really tracheæ. The greater number examined were found to communicate directly, therefore the others, having the same appearance in other respects, are supposed to agree also in this one.

In the literature on this subject, examples are given of one year's stems of certain Cruciferæ which contain no medullary rays, but these cases of *Veronica*, *Chelone* and *Digitalis* appear to be the first ones found where wood parenchyma also fails. It is the more remarkable as in other genera of the same family well developed and complex forms occur.

It is conceded at the outset that there is ground in the foregoing pages for the following objection, namely: That the hypothesis of a functional difference between bordered and simple pores is here based mainly upon another supposition, that of the water transport through the cell-lumen, which is itself only a supposition, and has yet to be substantiated by proof.

This objection, however, cannot be urged against the consideration of the question simply from the anatomical-systematical standpoint. It must be conceded, that without regarding this supposed function of the pores, a certain interest attaches itself

to the question how far this anatomical difference, that is, the presence or absence of the *border* in the libriform tissue, coincides with the morphological characteristics which decide the limits of genera, families and groups in our present system of classification.

Specimens from nearly all the genera of the large and most important dicotyledonous families were studied and compared in reference to this question. Some few of these families contain only two or three genera with woody tissue; of others only a few species were available, but the greater number of the families given in the following list were exhaustively examined.

With this examination we begin by comparing the genera of the different families, as there is no question in regard to the similarity of anatomical structure, in this respect, between the different species of the same genus.

Genera from sixty-one principal and six sub-families were examined with the results shown in the following tables; the sub-families are given here separately owing partly to the large number of genera some contain, and partly on account of certain differences in structure which incline botanists to regard them as distinct families.

FAMILIES WHOSE LIBRIFORM CONTAINS ONLY SIMPLE PORES.

Anacardiaceæ.	Corylaceæ.	Polemoniaceæ.
Araliaceæ.	Euphorbiaceæ.	Plumbagineæ.
Acanthaceæ.	Ebenaceæ.	Primulaceæ.
Anonaceæ.	Juglandaceæ.	Rutaceæ.
Acerineæ.	Labiatæ.	Rhamneæ.
Ampelideæ.	Lobeliaceæ.	Salicineæ.
Borragineæ.	Lauraceæ.	Selagineæ.
Bignoniaceæ.	Moreæ.	Ulmaceæ.
Betulaceæ.	Myrsineæ.	Umbelliferæ.
Berberideæ.	Meliaceæ.	Verbenaceæ.
Compositæ.	Papilionaceæ.	Valerianaceæ.

FAMILIES WHOSE LIBRIFORM CONTAINS ONLY BORDERED PORES.

Apocynaceæ.	Gordeniaceæ.	
Asclepiadeæ.	Magnoliaceæ.	SUB-FAMILIES.
Cornaceæ.	Proteaceæ.	
Dipsaceæ.	Plataneæ.	Dryadeæ.
Epacrideæ.	Rhodoraceæ.	Pomeæ.
Ericaceæ.	Staphylaceæ.	Roseæ.
Empetraceæ.	Vaccinieæ.	
	Styraceæ.	

FAMILIES WHOSE LIBRIFORM CONTAINS BOTH KINDS OF PORES.

	SUB-FAMILIES.
Campanulaceæ.	
Celastraceæ.	
Fagaceæ.	Amygdaleæ.
Sapotaceæ.	Spireæ.
Myrtaceæ.	Buxaceæ.

FAMILIES WHOSE GENERA DO NOT AGREE IN REFERENCE TO THE PORES.

Caprifoliaceæ.	Scrophulariaceæ.
Oleaceæ.	Solanaceæ.
Ranunculaceæ.	Tiliaceæ.
Saxifragaceæ.	Zygophylleæ.

By comparing these results in reference to the families of different groups, it will be seen that the idea of relationship between these families is not sustained by a correspondence in the anatomical structure of the libriform tissue.

In the group Labiatifloræ, for example, we find the families Labiatæ, Bignoniaceæ, Acanthaceæ and Verbenaceæ all contain libriform, with only simple pores; Globulariaceæ, which according to some authors belongs in this group, has at least one example, namely, *Globularia* with only bordered pores, while Scrophulariaceæ contains genera which do not agree in this respect, that is, some genera contain both bordered and simple pores, others only simple pores. The remaining two families usually included in this group, viz.: Plantagineæ and Lentibulariaceæ, were not examined, as they contain but few plants with well-developed woody tissue.

Of the families of another large group, Rosifloræ, we find Pomeæ, Roseæ and Dryadeæ agree in possessing pores with borders, while Spiræa and Amygdaleæ have both kinds. Of this group Poterieæ, Quillajeæ and Chrysobalaneæ were not examined.

In a number of other groups we find the same difference existing between the families composing them, and sometimes even between those families in which a certain degree of relationship is a well established fact; for example, Compositæ and Dipsaceæ, the former having simple, the latter bordered pores. So also with Anonaceæ and Magnoliaceæ.

On the other hand, there are two small groups whose members agree; these are Primulineæ, containing the families Prim-

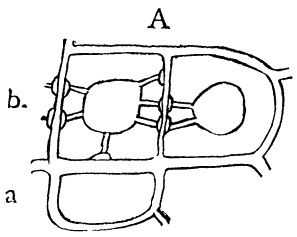
ulaceæ, Myrsineæ and Plumbagineæ, all of which have only simple pores. The second group is Bicornes, containing Epacrideæ, Ericaceæ, Vaccineæ, Rhodoraceæ and Hypopityaceæ, which contain only bordered pores. The latter family is not given in the list, because the only representatives of this family which were examined are placed by Bentham and Hooker in the family Ericaceæ

These examples are perhaps sufficient to verify the statement made in reference to the classification of families. In regard to the agreement of genera, the tables show without further explanation that the genera of thirty-three families agree in having only simple pores; of eighteen in having only bordered; of eight in having both kinds, while out of the whole number, sixty-seven, only eight are found where genera do not agree. A further description of these eight families will show that in most instances the morphological-systematic characteristics fail to indicate a very close relationship.

In the family Oleaceæ, three genera by some authors considered as sub-families, viz.: *Syringa*, *Ligustrum* and *Fraxinus*, vary from each other not only in regard to the presence or absence of the border, but also in other respects. In *Syringa* the libriform tissue contains pores with unusually large well-developed borders. *Fraxinus* has libriform with only simple pores, while *Ligustrum* has both kinds. The two latter genera differ widely in regard to the other elements of the woody tissue. That is, *Ligustrum* represents the most complex type, *Fraxinus* the most simple. Specimens of both were treated with Schultze's macerating solution, and in *Fraxinus* only tracheæ and simple-pored libriform were found. (Wood parenchyma and medullary ray cells are also present, as in all examples given where no special reference is made to them.) In *Ligustrum*, on the other hand, are found all the varieties of wood elements. As no systematist claims for these two genera a very close degree of relationship, this difference in anatomical structure is not so striking. *Forsythia* has large and well-developed borders in the pores of the libriform tissue.

A parallel case is found in the family Saxifragaceæ, so far as the libriform is concerned. *Philadelphus* has only bordered-

pored libriform, *Ribes* has both kinds. These two genera, however, present such morphological differences as to be classed by some authors in separate families. *Hydrangea* and *Deutzia* have bordered pores. In *Deutzia* the borders are not as large as in other genera, but the pores are very numerous, several lying on the same wall of a cross-section, as seen in fig. A.



Deutzia.—b—Libriform cells. a—Cells of the medullary ray.

Of Zygophylleæ only a few specimens could be obtained. Of those examined, *Tribulus* has only simple, *Guaicum* only bordered, and *Zygophyllum*, both kinds of pores.

In Ranunculaceæ, *Clematis* has only simple pores (these, however, are very numerous), while *Adonis* and *Pæonia* have bordered pores.

In Tiliaceæ, the genus *Corchorus* has libriform pores possessing borders of medium size. The other genera examined contain only simple-pored libriform. In Caprifoliaceæ, *Viburnum* has only bordered, *Sambucus* only simple pores.

This leaves only two more families belonging to this category, viz: Solanaceæ and Scrophulariaceæ. All the genera examined of the family Solanaceæ, except *Brunfelsia* and *Franciscea*, agree in having simple-pored libriform. These two genera have both kinds of pores in this tissue, the bordered element predominating over the simple. Endlicher classes these two genera with Scrophulariaceæ. With the members of this family they agree not much better, though one genus of Scrophulariaceæ examined contains both kinds of pores. Also the different genera of Scrophulariaceæ vary from each other in the number of elements of the woody tissue much more than those of Solanaceæ. This is so striking as to deserve particular mention.

As before stated, all the genera of the family Scrophulariaceæ, examined except *Freylinia*, contain libriform with only simple pores. In *Veronica*, *Chelone* and *Digitalis*, tracheæ and libriform cells form the entire woody tissue. We have previously mentioned *Veronica* as being the only example where both medullary rays and wood parenchyma cells fail. This is not strictly true,

for *Chelone* and *Digitalis* both have the same structure, viz: only tracheæ and libriform, but in these cases the stems examined were of only one year's growth and the woody portion not well developed; the specimen of *Veronica Andersoni* on the contrary, was a fair example of woody development. In *Halleria*, *Celsia*, *Scrophularia* and *Scoparia*, in addition to these elements, medullary-ray cells occur, but no wood parenchyma. In *Paulownia* and *Diplacus* the wood parenchyma is added; in *Paulownia* this surrounds the large tracheæ, no small ones occur. In *Diplacus* the larger tracheæ lie in radial rows along the medullary rays, thus in both instances the tracheæ are in connection with living, acting cells. In *Freylinia* the libriform contains both bordered and simple pores, the former predominating; all the other elements belonging to the most complex type are also found here, unless it may be the thin-walled tracheids, as it is not possible always to decide between these and the small tracheæ. So here we have a most marked contrast to the simple structure of the woody tissue of *Veronica*.

This variation of structure in the genera of a few families presents a striking contrast to the uniformity prevailing in the great majority. While it suggests at once the idea that the degree of relationship between the members of those few families may be very remote, still in those instances where this idea is not substantiated by corresponding morphological differences, as in case of the last family described, the possibility of transition stages in the development of the border naturally suggests itself.

Assuming only what is self-evident in reference to the function of the pores, that is, that they are designed to allow a freer communication between the cells than the walls otherwise furnish, we may suppose that in case of increased demand in this respect there might gradually occur a corresponding change in the form, size, or frequency of the pores to meet this demand.

First, as regards the form, it is possible that in this way the simple pore with its funnel-shaped enlargement at the base may, by a succession of changes, have developed into the bordered pore, the curve of the enlargement having grown more and more defined until at last it has changed into a decided angle. The attempt to verify this supposition by observation is, of

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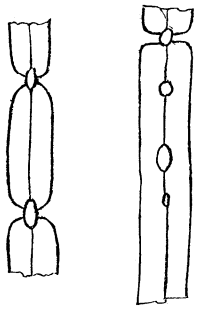

course, entirely impracticable. There is possibly a suggestion of such transition in the genus *Liriodendron*, B, before referred to, where the *borders* in the same cell were found to vary a little in form, some having the typical lenticular form, others inclining more to a circular shape. This, however, can be considered only as a suggestion.

It is, however, quite different when the question of size alone is considered. Several families were found in whose different genera all variations in the size of the border occur. For example, the family Ericaceæ, of which the genus *Erica* offers, perhaps, the best example found of this supposed beginning stage of the border. Here the form corresponds exactly with those found in the other genera, and we can trace the increase in size from one genus to another till we reach the genera *Vaccinium* and *Oxycoccus*, where the border attains a medium size.

In other families there was found great variation in the number as well as size of the pores. In the genus *Drimys* of the family Magnoliaceæ, the number of pores is about as great as the surface of the cell wall will allow, and the border quite as large as in some of the conifers. In *Illicium* the pores are considerably less frequent and the border nearly one-half smaller. In *Liriodendron* aud *Magnolia* the pores are so few in number and the border so small that they may easily be mistaken for simple pores. The difference in regard to the number of elements was also quite suggestive in these genera. In *Drimys*, where the borders are so large and so numerous, very few tracheæ occur, and none whose diameter exceeds that of the libriform cells. *Illicium* and *Liriodendron* contain a large number of tracheæ of different diameters and a smaller amount of wood parenchyma. These variations appear very striking when compared with the uniformity found in other families.

In conclusion, one more family may be referred to, whose genera contain both simple and bordered elements in the libriform tisssue in such variable quantities as to render it an exception to most other families: this is Myrtaceæ. As before stated,

Myrtus forms an exception to all the other genera by the absence of, at least, any visible simple-pored libriform. In *Eucalyptus globulus* a few cells only were found to contain simple pores. In *Eucalyptus perfoliatus* the number of cells containing simple pores is much greater; in a number of other genera, *Leptospermum*, *Melaleuca*, *Metrosideros*, *Eugenia*, etc., the quantity of each element is about the same.

From this somewhat cursory survey of the various families and groups, the conclusion reached is, that there is a certain parallelism between this peculiar anatomical structure and the morphological-systematical characteristics which decide the limits of the family, the principal cases which furnish exceptions to this statement being themselves genera of doubtful character.

Outside the limits of the family, however, this parallelism does not exist. That is to say, while the families of two or three groups were found to correspond in this respect, the greater number of groups showed no such correspondence in the structure of the libriform tissue.

A few words of explanation are necessary in regard to the terminology used in speaking of the various elements of the woody tissue. No particular system has been followed, not from any lack of systems, but rather from the opposite reason. Nearly every writer on this subject suggests a special method of classification. Of all the different articles on woody tissue that of Sanio is perhaps the most thorough and exhaustive. His method of classification is extremely difficult to use, as will be seen by the following explanation. He divides the wood elements, whose long axes are parallel with the long axis of the stem, into three classes: parenchymatic, tracheal and libriform elements. He distinguishes the tracheids from the bordered-pored libriform cells by the difference in the size of the border, and further, he says the real libriform cells never have spiral thickenings, which are almost always present in the tracheids. As they are not always present, and as he gives no concrete example which may be taken as a measure for the size of the border when we wish to decide whether a cell is to be classed with the tracheal or libriform element, we have no means to determine definitely.

A more recent article has appeared, " Vergleichende anatom-

ische Untersuchungen über die Differenzen im Primärem Bau der Stengel und Rhizome Krautartiger Phanerogamen" by Wladyslaw Rothart, in which the author suggests a principle of classification which he says rests on a morphological-anatomical basis, and claims for this method a great superiority over that based on the physiological-anatomical characteristics. He states expressly that in this system the mischievous practice of considering the probable function of an element in deciding to which class of tissue it belongs has been carefully avoided.

According to this author the wood elements are first divided into two classes, Desmogen and Bythom, or "strang" and "grund" tissue. The former he divides into four classes, the latter is not divided. Only the first two divisions of the Desmogen are of interest in this connection, namely: Inom and Tracheom. As Inom are considered all those desmogenic elements containing simple pores or none. As Tracheom all those containing bordered pores; this class includes the ring and spiral, as well as the "netz-gefässe," (reticulated tracheæ) the ring and spiral wall-thickenings being considered only modifications of the bordered pore, and the reticulated tracheæ a transition form between these two. This division is based principally on the common sculpture of the cell wall, which he says may be considered an infallible criterion.

It is well known that in many instances a single member of a trachea which borders on other tracheæ as well as on cells of the medullary ray and libriform tissue contains large and numerous bordered pores on the side adjacent to the other tracheæ, while that part of its wall bordering on the cells of the medullary ray or libriform tissue contains simple pores, and these in comparatively small numbers. In these cases the infallibility of the wall-sculpture does not appear sufficient to decide the class to which the element belongs. Very often in the course of this work were found single tracheal tubes; that is, a tube consisting of many members was found isolated from other tracheæ, and as far as could be traced it contained only simple pores. It is not improbable that where such tubes joined other tracheæ otherwise than by a dissolved partition wall, the usual bordered pores occurred, but as far as the section extended these members were entirely

isolated from other tracheæ and contained, as before mentioned, only simple pores. Here it is equally difficult to decide to which class this belongs. According to the wall-sculpture, it must be ranked with the thick-walled, closed, libriform cells, a classification which to us appears quite as unnatural as any of those based upon the probable function of an element.

Therefore, as no better method suggested itself, the generally conceded functions of the woody tissue were taken as a basis for division, viz: to furnish a means for the transport of water and to give strength and solidity to the stem. According to this idea, the different elements treated have naturally grouped themselves into two classes: those whose walls are so thin as to preclude the idea that they are of use as strengthening-cells, and those which, according to their anatomical structure and all the facts gained by experiment, may serve in both capacities, but more especially as strengthening-cells.

By speaking of this as a method of division, it is not meant that it furnishes an exact criterion, but only that it avoids the necessity of one. Where the various facts concerning an element lead to the conclusion that its principal function is that of a water carrier, this element is referred to as tracheal; where the facts point to the opposite conclusion the element is considered libriform. According to this view the bordered pore is considered a peculiar organ of the water-transporting elements, and whenever it is found in the thick-walled cells its presence is supposed to indicate that these cells undertake both functions of the woody tissue.

Since the completion of the foregoing pages, an article, "Ueber den Systematischen Werth der Holzstructur bei den Dicotyledon," has appeared, by Dr. Hans Solereder, Munich, in which this difference in the libriform tissue has been studied in a much larger number of families than the time and material for the present work has allowed. As the author only includes this among all the various other anatomical characteristics of the dicotyledonous woods, with no reference to any possible physiological meaning, he has, naturally, taken a different standard for the bordered pore, namely: the size of the border, and says wherever the border is larger than the "*spalt*" the pore may be

considered bordered. As this definition is sometimes difficult of application, he overcomes this by placing some families with small and imperfectly developed borders in the list with those containing only simple pores.

In this way it happens that the tables given by this author do not always agree with those of the present paper. For example, *Betula* and *Alnus* he gives among the bordered pored, although explaining that the border is here generally smaller than the "spalt." Also the pores of the libriform of *Fraxinus* he says possess "deutliche" borders, although smaller than the "spalt." Several other instances occur where the different standards taken to decide what a border is, cause a difference in the classification.

This indicates, however, no real difference in opinion, as the definition is simply arbitrary in both cases, and in instances like *Betula* and *Alnus*, the test of the angle between the tube and the border-opening was extremely difficult of application. Certain species of *Alnus* were examined where, had the decision rested on single cases alone, these must have been included in bordered-pored libriform.

It is hardly necessary to add in conclusion that the probability of the hypothesis assumed in the foregoing pages would be greatly strengthened by experiments proving that water, when forced by artificial means though a piece of wood consisting of bordered-pored libriform, passed through more readily than through wood containing only simple-pored libriform. Several experiments of this kind were tried at different times in the laboratory of Prof. Schwendener of Berlin, and also in that of Prof. Cramer at Zürich, the results of which were partially successful. It is hoped that these results may be verified and the experiments extended so far as to render them of sufficient interest for future publication.

Time of Fruiting of Buxbaumia aphylla.

In December of 1884 I noticed two patches of this interesting moss growing near Hamden Swamp, in the vicinity of New Haven, Conn.

My attention was first attracted by the bleached empty capsules of the preceding year's growth. One patch was situated near a decayed stump, the other at the foot of an oak. The soil